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Inter-attribute tilt effects and orientation analysis in the visual brain

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Abstract

A test grating appears to be tilted away from an inducing grating for small angular separations (repulsion), but towards the inducing grating for larger angular separations (attraction). Previous research on luminance gratings suggests that repulsion is caused by local inhibition in cortical areas V1 and/or V2, and that the attraction involves global interactions beyond V1, in extrastriate areas. Experiments reported here demonstrate attribute invariant attraction and repulsion effects for gratings specified by luminance, motion, and disparity contrasts. A frame surrounding the inducing grating abolishes only the attraction effect, but a spatial frequency difference, or a small gap between the inducer and test gratings, abolishes only the repulsion effect, irrespective of the attributes that specify the gratings. It is proposed that detectors selectively sensitive to attribute invariant orientation and size exist in early cortical sites such as V1 and/or V2.

Keywords: Contour; Cue invariance; Tilt illusion; Orientation

1. Introduction

Discontinuities (edges) in projected retinal images carry information about occlusion relationships corresponding to objects in the world. The segmentation of images by outline contours mediates a substantial amount of information for successful object recognition, and three-dimensional shape perception (Biederman & Ju, 1988; Christou, Koenderink & van Dorn, 1996). These processes are invariant to the information-bearing media, or stimulus attribute, in which the outline contour is specified (e.g. Carman & Welch, 1992; Sary, Vogels & Orban, 1993). Distal occlusion relationships typically generate image discontinuities in several attributes, e.g. luminance, colour, motion, texture, and binocular disparity. Luminance contours alone on the retina are ambiguous since they may be generated from distal configurations other than object boundaries and sharp foldings of surface orientation, e.g. shadows or speckled surfaces (Jakobsson, Bergstrom, Gustafsson & Fedorovskaya, 1997). Even if luminance contours and motion contours are signalled in conjunction from the same patch in the visual field they may be ambiguous, due to a moving object or a moving shadow. Nevertheless, as the number of attributes that signal a discontinuity increases, the likelihood that the discontinuity originates from the outline of an object is increased. Thus, it would be advantageous for the visual system if discontinuities from as many attributes as possible could be pooled together before further form estimating processes take place.

Tilt illusions offer important clues to unravelling interactions between mechanisms of contour orientation analysis for different stimulus attributes. They refer to misperceived orientation of lines in the frontoparallel plane due to either simultaneously present nearby inducing lines having a different orientation (simultaneous tilt effect, Gibson, 1937), or due to prior adaptation to inducing lines with a different orientation (successive tilt effects, Gibson & Radner, 1937). The test lines appear rotated away from the inducing lines if the angular separation is between 0 and 50°, producing contrast effects or repulsion. For separations between 50 and 90°, the test lines appear rotated towards the inducing lines, resulting in assimilation effects or attraction (Gibson & Radner, 1937). The tilt effects are similar in both simultaneous and successive induction

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situations (O'Toole & Wenderoth, 1977). These effects occur whether the contours are defined by luminance contrasts or if they are illusory (van der Zwan & Wenderoth, 1995).

Common mechanisms are thought to mediate both the simultaneous and successive tilt effects (Blakemore, Carpenter & Georgeson, 1970; Magnussen & Johnsen, 1986; Tolhurst & Thompson, 1975; Wenderoth, O'Connor & Johnson, 1986; Wenderoth & Johnstone, 1988a,b). Blakemore et al. (1970) suggested an explanation of these effects in terms of lateral inhibition between orientation-selective neurones in area V1, as described by Hubel and Wiesel (1962). It is assumed that neural populations, signalling different orientations at nearby spatial locations, inhibit each other. The inhibition has a repulsive effect on the peaks of activity in orientation space when a typical simultaneous tilt-inducing grating is presented. The successive tilt effect is accounted for by the Blakemore et al. model if the inhibition is tonic (Wenderoth & Johnstone, 1988a,b). Carpenter and Blakemore (1973), and Howard (1982) have substantially supported this view.

However, different mechanisms seem to mediate the repulsion and attraction occurring in both simultaneous and successive induction conditions. Wenderoth and Johnstone (1987) have related psychophysical data concerning simultaneous and successive tilt effects to cortical single cell functional organisation in what they call a kind of 'psychoanatomy'. First, repulsion but not attraction can be abolished when a gap of the order of 1° separates the inducer and test stimulus. This effect appears both for luminance contours (Virsu & Taskinen, 1975; Wenderoth & Johnstone, 1988a; Wenderoth, van der Zwan & Williams, 1993), and illusory contours (van der Zwan & Wenderoth, 1995). Attraction but not repulsion is abolished when a frame of reference surrounds the stimulus field for both luminance (Kohler & Wallach, 1944; Wenderoth & Johnstone, 1988a) and illusory contours (van der Zwan & Wenderoth, 1995). Repulsion is reduced if the spatial frequencies of the test and inducing gratings differ (Georgeson, 1973; Ware & Mitchell, 1974) but not attraction (Wenderoth & Johnstone, 1988a). Likewise, repulsion is reduced when reducing the outside diameter of the annulus surrounding the test grating, but not attraction (Wenderoth & Johnstone, 1988a). The temporal characteristics of the repulsion effect differ from those of attraction: repulsion reaches a peak at about 25 ms and levels out to reach an asymptote after 100 ms, whereas attraction levels out to reach an asymptote at exposures of about 400 ms (Wenderoth & Johnstone, 1988b).

Results from binocular rivalry experiments suggest that the rivalry occurs in V2, and provide support for the claim that the attraction effect is mediated by activity in area V2 or beyond (van der Zwan & Wenderoth, 1994). Wade and Wenderoth (1978) found that binocular rivalry during adaptation to a grating tilted 10° from the vertical caused no change in the magnitude of the repulsion tilt aftereffect. They concluded that the processes mediating the aftereffect seemed to occur before those mediating binocular rivalry. van der Zwan and Wenderoth (1994) replicated this finding but showed that when the tilt of the adaptation line was 75° from the vertical, then rivalry reduces the attraction tilt aftereffect. Also, when a subjective contour was adapted to, then rivalry disrupted both the attraction and repulsion effect. Inhibitory interactions between orientation selective cells in visual area V1 have been suggested to account for the tilt effect (Carpenter & Blakemore, 1973), and visual area V2 to mediate perceived subjective contours (von der Heydt & Peterhans, 1989).

The double dissociation found for repulsion and attraction effects have been taken as evidence that they are caused by different processing strategies taking place in different neural populations. The strategies differ with respect to the direction of the tilt induction and the spatial extent of the interactions between the gratings. Whereas mechanisms mediating repulsion are local in character, attraction effects require global pattern selective mechanisms (e.g. Wenderoth & Johnstone, 1988a,b). In this view, repulsion arises partly from local lateral inhibition between simple spatial frequency and orientation selective cells like those in area V1, whose response characteristics match those of the repulsion effect. These data also support the idea that the perception of subjective contours and real contours is mediated by activation of cells with properties that are typical for cells in early visual areas (von der Heydt & Peterhans, 1989). Accordingly, cells in cortical area V2 have been shown to respond to both real and illusory contours with similar orientation preferences (von der Heydt, Peterhans, & Baumgartner, 1984). Dresp and Grossberg (1997) demonstrated that thin subthreshold lines summate with illusory contour so that the illusory contour becomes more discriminable, providing psychophysical support for the idea that illusory and real contour perception is mediated by common neural substrates.

Attraction, on the other hand, has been proposed to be mediated by mechanisms performing global orientation analysis, and supposed to occur in extrastriate regions where there are neurones whose responses are affected by global stimulus properties (e.g. Wenderoth & Johnstone, 1987). Others have shown that global processing, such as figure ground segmentation from motion and texture discontinuities, can be accomplished in area V1, mediated by interconnected distant neurones, or by feedback from extrastriate areas (Lamme, van Dijk & Spekreijse, 1993a,b). Even though the neural underpinning for the attraction and repulsion may share common cortical areas, the double dissociation experiments of Wenderoth and Johnstone (1988a) provide evidence for different processing strategies, or for highly non-linear processing.

Many attempts have been made to determine the degree of interaction between contours defined by various attributes, by using cross adaptation procedures (e.g. Smith & Over, 1975; Tyler, 1975; Favreau, Flanagan, & Cavanagh, 1988; Cavanagh, 1989; Flanagan, Cavanagh & Favreau, 1990). Berkeley, DeBruyn and Orban (1994) found cross adaptation effects for all combinations of illusory, motion, and luminance defined contours, suggesting contour attribute invariance. They did not investigate inter-attribute attraction effects since their adaptation gratings had tilts ranging between 0 and 50°, and attraction occurs only for larger tilts, and it was beyond the scope of their investigation to investigate the dissociation between attraction and repulsion for the various attributes.

Here I will use the simultaneous tilt effect as a probe in an attempt to detect interactions and possible sites of orientation integration across luminance-, motion-, and disparity-defined contours in the visual system. The first aim is to see if attraction and repulsion effects can be obtained when gratings defined by other attributes than luminance are used (intra-attribute conditions). The second aim is to investigate the inter-attribute properties of contour interactions. The third aim is to unravel possible sites of attribute integration. Psychophysical data concerning repulsion and attraction for luminance defined gratings has been successfully related to single cell functional organisation. Possible sites of integration may be found by manipulating the stimuli in ways known to reduce repulsion but not attraction effects (for luminance gratings), or vice versa.

2. General methods

2.1. Apparatus and stimuli

The stimuli consisted of an inner circular test grating surrounded by the inducing annulus grating. A computer program was developed to create images of gratings defined by luminance, motion, and disparity. The image for the right eye was displayed on the left side of the screen, and the image for the left eye was displayed on the right side. A polaroid filter stereoscope was used to facilitate binocular fusion of the stereoimages presented on the screen. An IBM compatible computer was used to display the stimuli on a 17-in. (1024×768) screen with refresh rate of 75 Hz. The viewing distance was 75 cm from the screen.

The inducing gratings were created before presentations and stored in the computer memory. The test patterns were created and displayed in real time so that the method of adjustment could be employed when setting the orientation of the test grating. Pressing either the right or the left arrow key could rotate the test grating clockwise or counter-clockwise, respectively. The rotation speed was 1.5°/s during continuous key press, and the rotation step 1/3° at brief key presses.

Luminance, motion, and disparity contours were used in pairwise combinations defining the test and inducing grating, resulting in nine different combinations of test and inducer. In three conditions (intra-attribute), the inducer and test were defined by the same attribute. In six conditions (inter-attribute), the inducer and test were defined by different attributes. The inducing gratings were confined to a circular area with a diameter of 8°. Each inducing grating was presented in seven different orientations ranging from vertical (0°) to horizontal (90°) in steps of 15°. A 1.5° central circular test grating was superimposed on the inducing grating with a central 1.5° blank aperture. Square wave gratings with a spatial period of 1.5° were used for all test and inducing stimuli, except for the luminance test grating. A sinusoidal luminance test grating was used to avoid effects of sawtooth edges for sharp luminance gratings, caused by the pixel-based display for oblique orientation settings, since this could have been used as a cue to non-vertical test settings. No sawtooth edges could be perceived in oblique settings of the smooth sinusoidal luminance distribution. The luminance gratings were dark grey on a dark background (Fig. 1A). The motion- and disparity-defined gratings were displayed in random dot fields. The dots were white and each dot had a width of 1.5 arcmin.

The motion-defined grating was created by relative motion in a random dot display with about 1500 dots (30 dots/square deg), so that no single frame in the motion sequence provided information about the contours. Bars containing stationary dots were spatially alternated with bars containing coherently moving dots. The stationary bars were perceived as occluding an oscillating background. The direction of motion of the background was always a sinusoidal translation back and forth along the horizontal regardless of the orientation of the stationary foreground grating (Fig. 1B). Thus, motion was orthogonal to the contour when vertical contour settings were displayed, and along the contour during horizontal contour settings. The motion amplitude was 0.4° and the frequency was 1.4 motion-cycles/s.

Binocular disparity in random dot stereograms (1500 dots) was used to define the disparity gratings so that no monocular information about the contours was available. The disparity for all disparity gratings was 10 arcmin, which created a clear impression of a grating hovering in front of a background when the stereopictures were fused (Fig. 1C). The test gratings were presented at the same stereoscopic depth plane as the stereoscopically hovering inducing grating. Similarly, the inducing gratings were presented at the same stereoscopic depth plane as the test grating when it was defined by disparity information.

2.2. Participants

Those observers that could not perceive the disparity gratings were excluded from participating in the experiments. Twenty-five naive undergraduate students that passed the test participated.

2.3. Procedure

The observer's task was to adjust the test grating as accurately as possible to the apparent vertical from an initially randomly chosen orientation ranging between − 30 and + 30° from physical vertical. Seven different inducer orientations combined with the nine combinations of the inducer and test attribute resulted in 63 stimuli; each stimulus was presented once to each observer. The order of presentation was randomised for each observer, and the sign of the tilt of the inducing contour was randomly assigned either clockwise or counter-clockwise direction. After adjustment of the test grating to the perceived vertical, by pressing the right or left arrow key, the observers pressed the space key so that the orientation of the test grating was saved in a datafile together with information about stimulus attributes and the orientation of the inducer. About 1–1.5 s break was allowed between successive stimulus presentations while the computer created 20 frames to be presented in a repeated sequence during the next stimulus presentation.

The observers participated in four experiments. Each experiment took about 20 min. Two experiments were completed in the same experimental session. The next experimental session, with the remaining two experiments, was performed on a separate day. The participants were familiarised with viewing the stereoimages through the stereoscope before the beginning of the first experimental session.

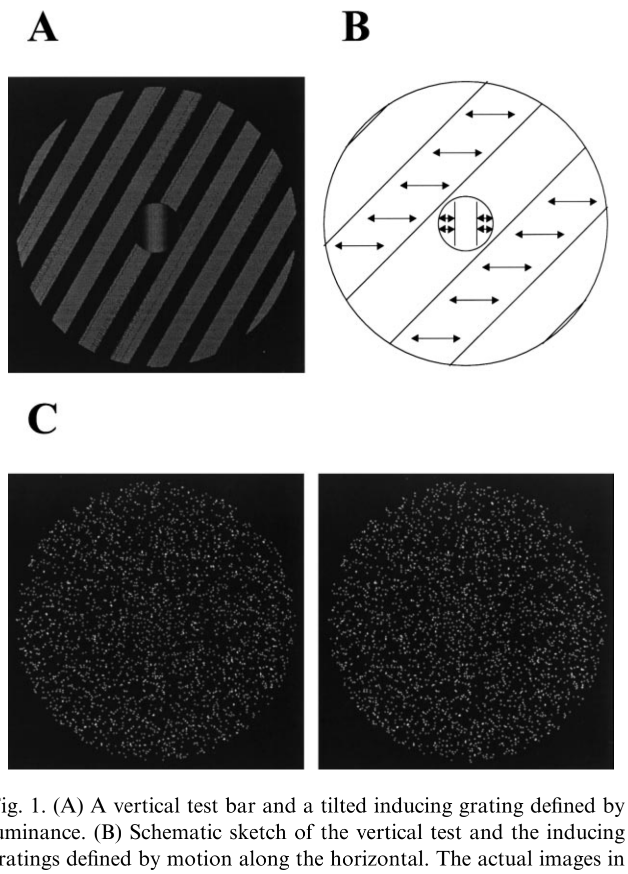


Fig. 1. (A) A vertical test bar and a tilted inducing grating defined by luminance. (B) Schematic sketch of the vertical test and the inducing gratings defined by motion along the horizontal. The actual images in the motion sequence were created by randomly positioned white dots on a dark background. Arrows show the direction of coherently moving dots between the fields of stationary dots. Although the lengths of the arrows in the test and inducing gratings are dissimilar, the amplitudes of motion were the same. (C) Grating defined by binocular disparity. The vertical test bar surrounded by tilted thick inducing bars hovering in front of a background is seen when the stereopictures are cross-fused. Uncrossed fusion reverses the depth relationships.

3. Experiment 1

One aim of this experiment was to investigate if repulsion and attraction effects can be demonstrated in intra-attribute conditions for attributes other than luminance. Another aim was to find out if repulsion and attraction could be demonstrated in inter-attribute conditions, with different attributes defining the test and inducing gratings. If the stimulus attributes (luminance, motion, and disparity) combine early, before lateral interaction, both repulsion and attraction will appear in all inter-attribute conditions. If the stimulus attributes combine after lateral interactions have taken place but before the occurrence of global interactions, then only attraction will appear and not repulsion. If the stimulus attributes combine after that the global analysis has taken place, there will be no tilt effects at all in the inter-attribute conditions. If local and global orientation analysis in visual cortex is performed in separate attribute-specific pathways then both repulsion and attraction effects are suspected to be attribute specific.

3.1. Results

The result from Experiment 1 shows that both attraction and repulsion effects exist in both intra- and inter-attribute conditions, although with different strengths (Fig. 2). Most settings of the test gratings are physically tilted towards the inducing grating to compensate for the orientation repulsion when the tilt of the inducer is 15 or 30° from the vertical. The setting of the orientation of the test grating is away from the

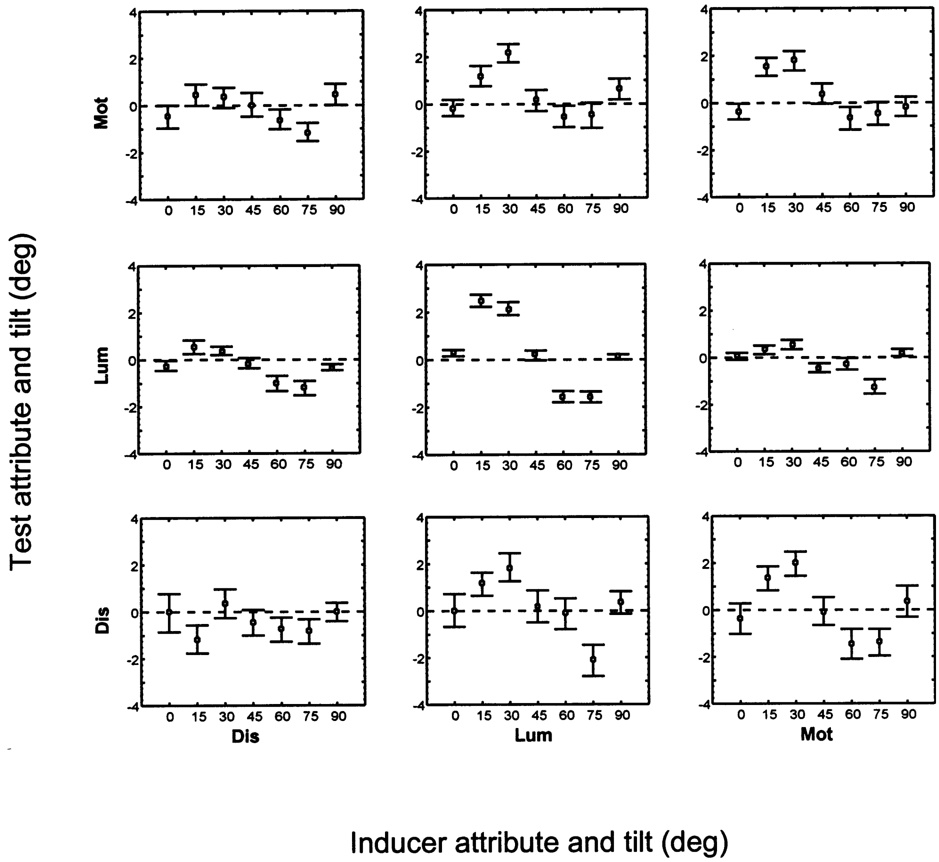


Fig. 2. The results from Experiment 1: test attributes and deviations of test orientation settings to the vertical are displayed on the vertical axes, and the orientations of the inducing gratings are displayed on the horizontal axis. Deviations are positive if they are in the same direction as the inducer tilt. Repulsion (inducer tilts 15 and 45°) and attraction (inducer tilts 60 and 75°) in various magnitudes occurs in both intra- and inter-attribute conditions. Mot, motion; Lum, luminance; Dis, disparity. Whiskers show ± 1 SE.

orientation of the inducer to compensate for the attraction when the inducer is tilted 60 or 75°. With luminance-defined test and inducing gratings the repulsion effect averaged 2.5° and the attraction effect averaged 1.5°. Luminance-defined inducing gratings generally yielded larger tilt effects. These inducing gratings also yielded the strongest contour salience. Previously it has been reported that reducing the salience of test contours increases the tilt repulsion aftereffect but the opposite occurs when the salience of the inducing contours are decreased (Berkley et al., 1994). The variation in the magnitude of the tilt effects for the various combinations of attributes might be due to corresponding variances in contour salience. Luminance-defined test gratings produced results with less variability than motion and disparity-defined bars. This might be due to the stochastic nature of the random dot displays used in the motion and disparity defined bars leading to less efficient orientation discrimination from these displays, and less perceived contour salience. It might also be due to rather coarse spatial resolution of perceiving disparity gratings (Tyler, 1974) and motion gratings.

4. Experiment 2

For luminance gratings it has been demonstrated that when a frame of reference surrounds the inducing grating, then attraction but not repulsion effects are reduced (Kohler & Wallach, 1944; Wenderoth & Johnstone, 1988a). The purpose of Experiment 2 was to examine if this phenomenon can be demonstrated with gratings of other attributes than luminance, and if it can be demonstrated in inter-attribute conditions. A luminous thin square frame (1 pixel width, side length 8°) surrounded the stimulus field adjacent to the inducing grating as a frame of reference. Other stimulus parameters were the same as in Experiment 1.

4.1. Results

The results of Experiment 2 (Fig. 3A) demonstrate selective reduction of the tilt attraction effect in both intra- and inter-attribute conditions (inducer tilts 60 and 75°), caused by applying a luminance frame surrounding the inducing grating. The magnitude of the repulsion (inducer tilt 15 and 30°) is not notably influenced by the presence of the frame. This supports that repulsion is of local character and that attraction involves global interactions. The luminance frame surrounding the stimulus field reduces attraction to various degrees for the different attribute mixtures (Fig. 3A) as compared to the results from Experiment 1, where no such frame was present (Fig. 2). The attraction effect is reduced from −1.5 to −0.7° when luminance defined inducing and test gratings are used. For

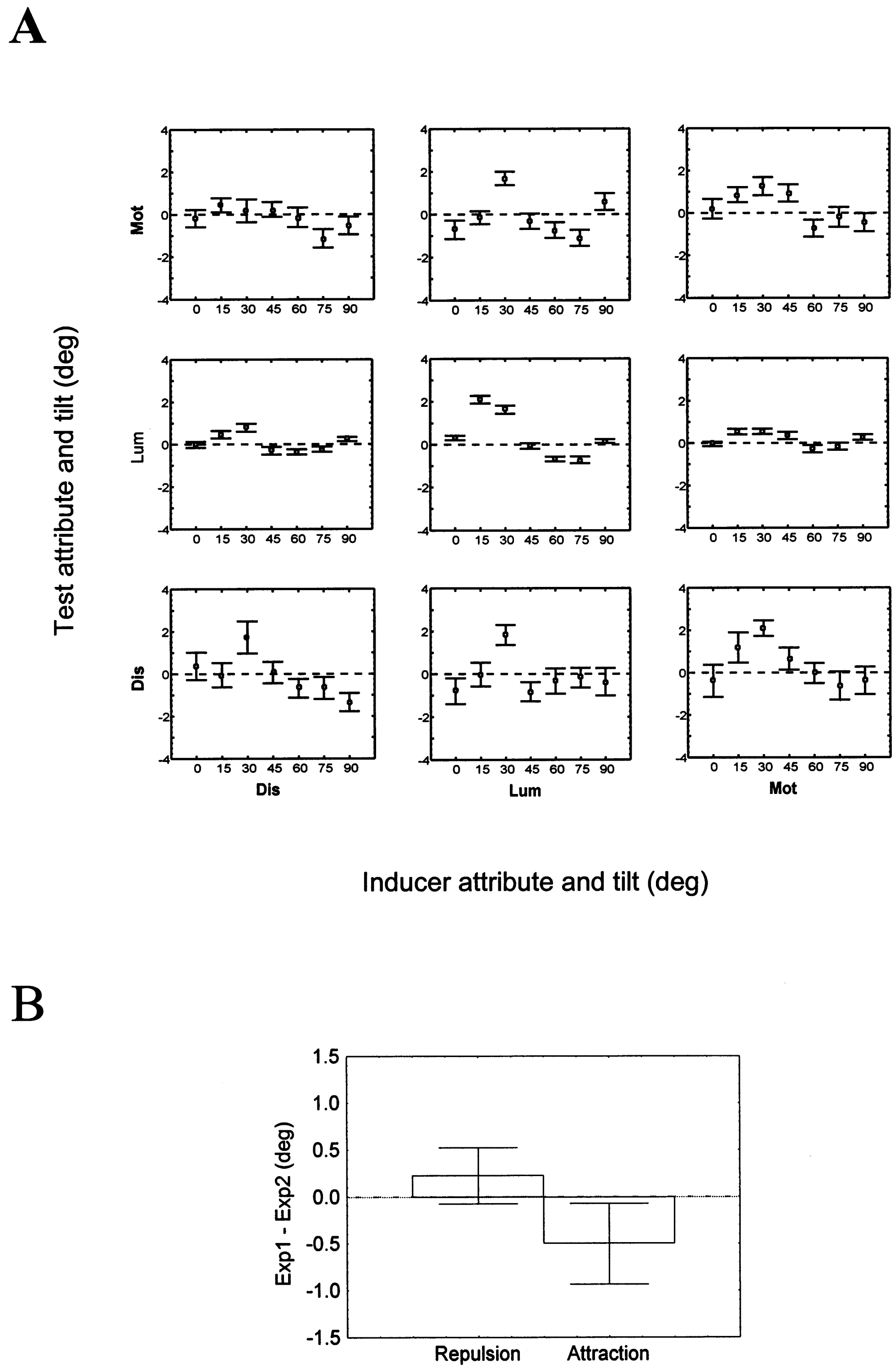


Fig. 3. (A) The results from Experiment 2: A luminous frame surrounds the inducing grating. The repulsion (inducer tilts 15 and 45°) as measured in Experiment 1 is unaffected by the frame in both intra- and inter-attribute conditions. The attraction (inducer tilts 60 and 75°) is diminished. Mot, motion; Lum, luminance; Dis, disparity. Whiskers show ±1 SE. (B) Mean differences of the results from the six inter-attribute conditions between Experiment 1 and 2. The repulsion and attraction conditions are displayed separately. Whiskers show 95% confidence intervals.

other attribute combinations, the attraction effect seems to be totally diminished even though the repulsion effect is not affected in magnitude compared to the corresponding repulsion effects from Experiment 1. The results in the six inter-attribute conditions in Fig. 3A are collapsed in Fig. 3B. The mean is shown of the differences between the inter-attribute tilt effects in Experiment 1 (control), and the inter-attribute tilt effects in Experiment 2 (frame), together with the 95% confidence intervals. The means are calculated across the 15 and 30° inducing tilt conditions (repulsion), and across 60 and 75° inducing tilt conditions (attraction) separately across all six inter-attribute conditions. The zero level in Fig. 3B is the baseline, indicating no difference between Experiment 1 and Experiment 2, that is, no effect of the frame. The mean difference between the inter-attribute repulsion conditions in Experiments 1 and 2 is 0.2°. The corresponding 95% confidence interval includes the baseline indicating a non-significant ($P > 0.05$) reduction of the repulsion effect when a frame is surrounding the inducing grating. The mean difference between the corresponding attraction conditions is $-0.5°$, which is 2.5 times greater than the reduction in the repulsion conditions caused by the surrounding frame. The corresponding 95% confidence interval does not include the baseline. Thus, the inter-attribute attraction effect, but not the repulsion, is significantly reduced ($P < 0.05$) when a frame surrounds the inducing grating compared to Experiment 1 when no such frame was presented.

5. Experiment 3

When using luminance gratings, repulsion but not attraction effects are diminished by introducing a 1° gap between the inducer and test gratings (Virsu & Taskinen, 1975; Wenderoth & Johnstone, 1988a; Wenderoth et al., 1993). The aim of Experiment 3 was to examine if similar effects are obtained in intra-attribute and inter-attribute conditions when using gratings defined by luminance, motion, and disparity. The stimulus settings were the same as in Experiment 1, except for the introduction of the gap between the inducing grating and the test grating. The gap size between inducing and test grating was 1°, so that the area of the inducer was reduced compared to the situation in Experiment 1.

5.1. Results

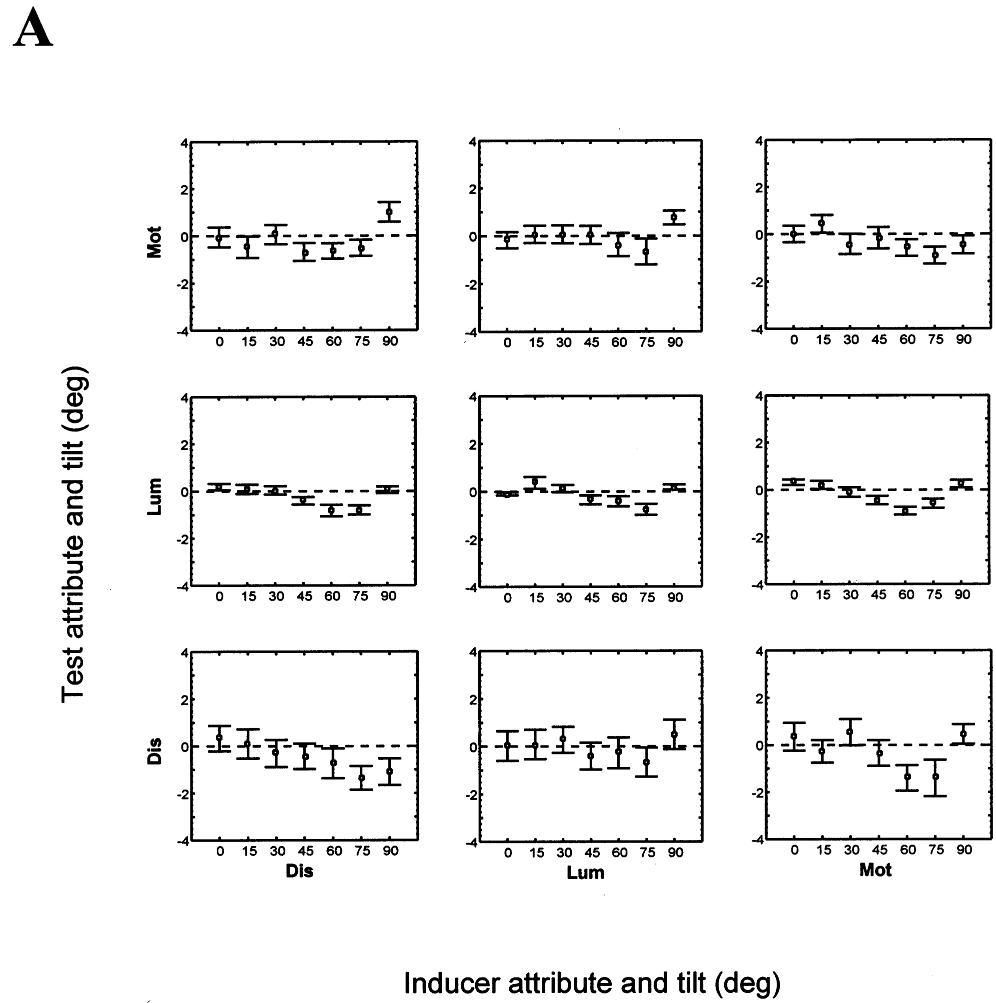
The results from Experiment 3 demonstrate that the selective impairment of the repulsion effect by spatially separating the inducer and test gratings occur in both intra- and inter-attribute conditions. A 1° spatial separation between the inducing and the test gratings efficiently eliminates repulsion (inducer tilts 15 and 30°) for all combinations of attributes (Fig. 4A). The attraction effect (inducer tilts 60 and 75°) persists, although considerably reduced when both inducing and test gratings are defined by luminance, as compared to the results from Experiment 1. The results in the inter-attribute conditions in Fig. 4A are collapsed in Fig. 4B. The mean difference is shown between the results from Experiment 1 (control) and Experiment 3 (separation) for the repulsion inducing tilts (15 and 30°) and the attraction inducing tilts (60 and 75°) over the six inter-attribute conditions, together with the 95% confidence intervals. The difference between the inter-attribute repulsion effects in Experiment 1 and Experiment 3 is 1°. The 95% confidence interval about the mean does not include the baseline (zero difference) indicating a significant ($P < 0.05$) reduction of the repulsion effect due to the spatial separation between the inducing and test gratings. The difference between the inter-attribute attraction effects in Experiments 1 and 3 is $-0.2°$ which is one fifth of the reduction of the repulsion effect. Also, the 95% confidence interval includes the baseline, indicating a non-significant ($P > 0.05$) reduction of the inter-attribute attraction effect. The results from Experiment 3 are consistent with previous results reported for luminance gratings.

6. Experiment 4

For luminance gratings, the repulsion effect is reduced when the spatial frequency of the inducer and test gratings differ (Georgeson, 1973; Ware & Mitchell, 1974; Wenderoth & Johnstone, 1988a). The aim of Experiment 4 is to find out if the repulsion is selectively reduced when the spatial frequency of the inducer and test gratings differ in intra- and inter-attribute conditions. The same stimulus settings were employed as in Experiment 1, except that the spatial period in the inducing grating was reduced to 0.4 c/deg so that the spatial frequency difference between inducing and test grating was about 2 octaves.

6.1. Results

A spatial frequency difference of two octaves between the test and inducing gratings efficiently abolishes the repulsion effects for all combinations of attributes, although not completely in the intra-attribute luminance grating condition (Fig. 5A). Fig. 5B shows the mean difference for the collapsed inter-attribute repulsion (15 and 30° inducer tilt) and inter-attribute attraction (60 and 75° inducer tilt) conditions between Experiment 1 (control) and Experiment 4 (frequency), together with the 95% confidence intervals. The inter-attribute repulsion is reduced 1° by the spatial



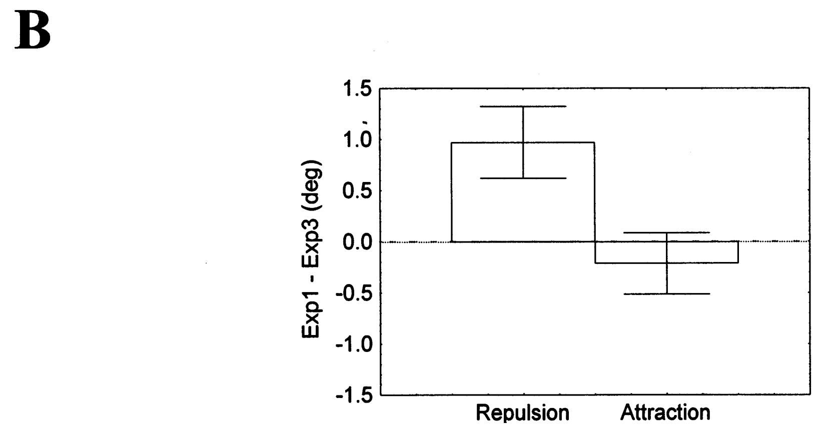


Fig. 4. (A) The results from Experiment 3: the test and inducing grating is spatially separated by 1°. The repulsion as measured in Experiment 1 (inducer tilts 15 and 45°) is demolished. The attraction (inducer tilts 60 and 75°) although reduced in magnitude is still present. Mot, motion; Lum, luminance; Dis, disparity. Whiskers show ± 1 SE. (B) Mean differences of the results in the six inter-attribute conditions between Experiment 1 and 3. Whiskers show 95% confidence intervals.

frequency difference between inducing and test grating. The positive attraction difference of 0.8° indicates an increase in the attraction effect caused by the spatial frequency difference (Fig. 5B). The corresponding 95% confidence intervals exclude the baseline, indicating that both effects are significant ($P < 0.05$). Similarly, Wenderoth and Johnstone (1988a) obtained a tendency for increased attraction effect when luminance gratings with a spatial frequency difference of 2 octaves were used in both inducer and test gratings. The attraction effect is strongly increased when low spatial frequency gratings of disparity or motion are used as inducers.

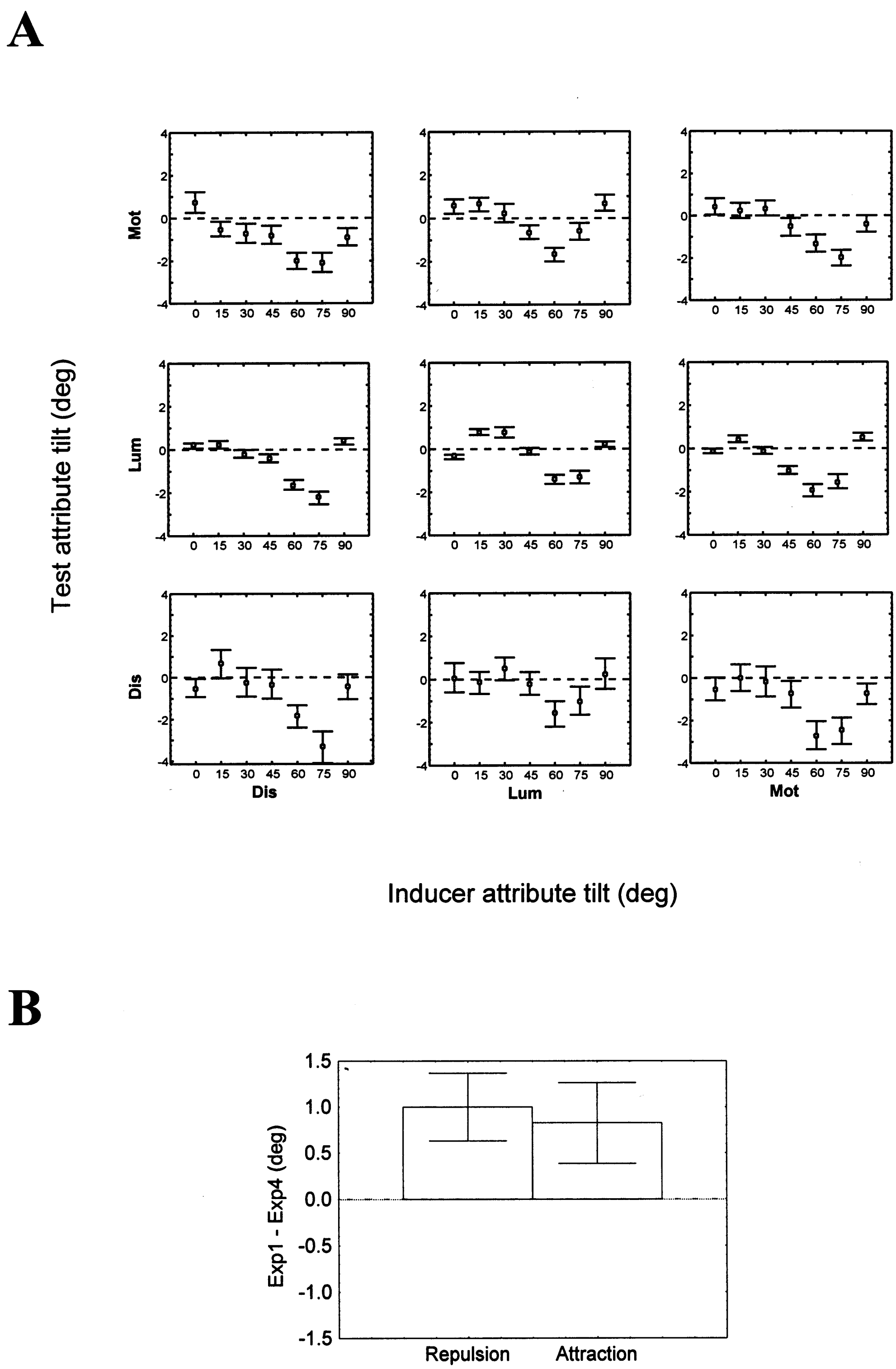


Fig. 5. (A) Results from Experiment 4. The spatial frequency is 2 octaves lower in the inducing grating than in the test grating. The repulsion effect (inducer tilts 15 and 45°) is efficiently diminished across attribute combinations. The attraction effect (inducer tilts 60 and 75°) is attenuated across attribute combinations compared to the results from Experiment 1 (Fig. 2). Mot, motion; Lum, luminance; Dis, disparity. Whiskers show ± 1 SE. (B) Mean differences of the six inter-attribute results between Experiment 1 and 4. Whiskers show 95% confidence intervals.

This result is consistent with the notion that the impression of contour salience for the motion and disparity gratings increases as the spatial frequency is decreased from 1.5 to 0.4°/cycle. The contour salience influences the magnitude of tilt effects (Berkeley et al., 1994). Accordingly, the perceptual sensitivity function for disparity-defined gratings seems to be bandpass with a peak at lower spatial frequencies than luminance gratings (Tyler, 1974).

Previously it has been shown that the simultaneous tilt repulsion effect is reduced when the spatial frequencies differ between the inducing and test gratings, but that the attraction effect is insensitive to such differences. Similar findings are shown in the result of Experiment 4. The lack of orientation repulsion due to spatial frequency difference between the inducing and test grating suggests that the local orientation interactions are spatial size selective. The repulsion is attribute invariant, but spatial frequency selective, across the various attributes defining the gratings. This means that spatial frequency selective tilt analysers pool information across attributes before any lateral interactions takes place between orientation analysers with similar size preferences.

7. Discussion

The strategies used to detect contours from luminance, motion, and disparity must involve qualitatively different comparator mechanisms. The detection of motion boundaries requires that information is compared over time, the detection of disparity contours requires that information is compared between the eyes, and the detection of luminance boundaries requires that information is compared over spatial positions in each eye. The results from Experiment 1 demonstrate attraction and repulsion effects in both inter- and intra-attribute conditions when luminance, motion, and disparity specify the contours. Even though the comparator mechanisms differ substantially between these attributes, the results show that their output is pooled before any lateral interactions take place, or that a single multi-comparator mechanism mediates contour detection. Experiment 2 shows that when a frame surrounds the inducing grating, attraction but not repulsion decreases in both intra- and inter-attribute conditions. Experiment 3 shows that a spatial separation between the inducing and test gratings decreases the repulsion but not the attraction effect in both intra- and inter-attribute conditions. Experiment 4 demonstrates that repulsion is spatial frequency (or size) specific across attributes, but that a spatial frequency difference has no effect on attraction. These results demonstrate that manipulations that selectively impair either the repulsion or the attraction of orientations are attribute invariant. The simplest interpretation of the result is that information about orientation, spatial size, and localisation is pooled across stimulus attributes before any lateral interaction takes place. Although others have found indications of independent orientation channels in the chromatic (two channels) and in the luminance (one channel) domain (Flanagan et al., 1990), the present results indicate that luminance, motion, and disparity may be strongly integrated.

The results demonstrate, in line with previous results, that the neural underpinnings of the repulsion and attraction effects are different, or that a highly non-linear mechanism mediates both effects. Repulsion is characterised by local inhibition between similar orientations and spatial scales across attributes, presumably at an early cortical site such as V1 or V2. Attraction is characterised by long range co-operation processes among similar orientations, or alternatively inhibition between dissimilar orientations across spatial scales and attributes, and might be localised in prestriate areas or due to the re-entrant activity (top-down) from higher areas to areas V1 and V2. There, local competition sharpens signals of orientation and location. For the first time, to my knowledge, inter-attribute spatial frequency selectivity is demonstrated in that the repulsion effect is attribute invariant but spatial frequency selective.

Previously, cross adaptation techniques have been used to investigate interactions between neural mechanisms that estimate contours from different attributes. Tilt aftereffects have been demonstrated in gratings defined by disparity in random dot stereograms, and transfer of adaptation has been demonstrated from luminance gratings to such stereogram gratings (Tyler, 1975). Since the tilt of the adaptation grating was varied between -50 and 50° only repulsion effects were observed. Tyler (1975) noted that adaptation to a disparity grating produces a spatial frequency shift when subsequently observing disparity gratings with a slightly different spatial frequency, similar to that obtained by adaptation to luminance gratings. He reasoned that the observation of spatial frequency shifts in any attribute may be taken to imply the existence of size-tuned channels. Both the classical motion aftereffect caused by adaptation to moving luminance contrasts (Cameron, Baker & Boulton, 1992) and the stereoscopic motion aftereffect are selective for spatial frequency and orientation (Shorter, Bowd, Donnelly & Patterson, 1999). The results from Experiment 4 reported here may be taken as further evidence for the existence of channels for luminance and disparity tuned to size or spatial frequency, and also that similar channels exist for motion-defined gratings. The results from Experiment 4 further show that the inter-attribute tilt repulsion is spatial frequency specific, which may imply the existence of attribute invariant detectors selectively sensitive to both size and orientation.

Rivest, Intriligator, Warner and Suzuki (1997) found shape contrast effects when the inducer and test shapes were either defined by the same or different attributes (colour and/or luminance). By using a perceptual learning paradigm Rivest, Boutet and Intriligator (1997) demonstrated improvements of contour orientation discrimination for bars defined by luminance, colour, and motion. The improvement was not restricted to the attribute used during training and it was retinotopic, suggesting that the training improves sensitivity of orientation selective cells responsive to contours defined by colour, luminance, or motion. Their results further support the notion that contour attribute invariant orientation detectors mediate visual performance in orientation detection tasks. Also, Rivest and Cavanagh (1995) found spatial interactions in a contour localisation task between all pairings of luminance-, colour-, motion-, and texture-defined contours.

Successive inter-attribute contrast phenomena similar to the tilt repulsion effect have been demonstrated in the perception of slant in depth, after adaptation to slant from motion, disparity, or texture. The slant aftereffect transfers from the test to the adaptation phase when a different attribute is presented in each phase (Graham & Rogers, 1982; Poom & Börjesson, 1999). Other inter-attribute visual phenomena include motion aftereffects (Patterson, Bowd, Phinney, Pohndorf, Bartonhoward & Angilletta, 1994), and motion repulsion aftereffects (Patterson & Becker, 1996) in that both transfer between stereoscopic and luminance domains. Also, inter-attribute apparent motion has been demonstrated (Cavanagh, Arguin, & von Grünau, 1989) that further supports early cue integration by psychophysical methods.

The results presented here show that the tilt illusions happens at attribute invariant levels, and these ought to be 'lower' than the well known attribute invariant shape recognition processes in inferior temporal (IT) cortex (Sary et al., 1993). Thus, cells in primate cortical area V2 respond to the orientation of contours from both relative motions and luminance (Marcar, Raiguel, Xiao, Maes & Orban, 1992), and cells in area V1 respond to stereoscopic boundaries (Poggio & Poggio, 1984; Poggio, Motter, Squatrito & Trotter, 1985). Also, cells selectively sensitive to the orientation of both real and illusory contours have been found in area V2 (von der Heydt et al., 1984). Thus, neurophysiological data together with the psychophysical results reported here supports the notion of contour-cue invariance in areas, such as V1 and/or V2.

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